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What is natural? The scale of cryptogenesis in the North Atlantic Ocean

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ABSTRACT

Aim Cryptogenic species may include those taxa that were historically introduced and are now falsely viewed as native. Investigated here is the scale of cryptogenesis in the North Atlantic Ocean by examining disjunct distributions, defined as temperate species occurring only on both sides of the North Atlantic. Disjunct distributions can be explained by four scenarios: glacial relicts, taxonomic artefacts, natural trans-oceanic dispersal and human-mediated introduction.

Location North Atlantic Ocean.

Methods Model taxa included ascidians, bivalves and hydrozoans. Biogeographic status (native, introduced or cryptogenic) was assigned to all species exhibiting a disjunct distribution, based upon multiple criteria.

Results Of 1030 species, 60 have a strictly disjunct distribution. Of these disjunct species, for five species there is no reason to doubt their native status, and 55 species are cryptogenic or introduced. Groups with high relative dispersal capacities do not have disjunct distributions more often. Infaunal bivalves have the lowest relative number of disjunct species; none are cryptogenic or naturally disjunct. This supports the concept that glaciations are unlikely to cause disjunct distributions: there are no studies that provide conclusive evidence for the glacial relict model. Hydrozoa have the highest relative number of disjunct species, which, while historically explained by undocumented rafting, may more likely be the result of dispersal by ships, which travel relatively fast, are independent of currents and provide greater surface area.

Main conclusions This reanalysis of the historical biogeography of the North Atlantic marine biota reveals that far more species may have been introduced than previously recognized, potentially significantly altering our fundamental understanding of community evolution and ecology. Species that have been present for centuries and can be important ecological engineers who have shaped contemporary communities are possibly falsely viewed as native: they may in fact be the unrecognized introductions of historical times.

Keywords

biological invasions, cryptogenic species, disjunct amphi-Atlantic distributions, dispersal, introduced species, post-glacial recolonization, ship fouling.

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INTRODUCTION

Biological invasions are one of the clear drivers of global change (Halpern *et al.*, 2008), with invasions rates in all environments having increased steadily in the past century (Cohen & Carlton, 1998). Strong evidence suggests that the number and rate of modern-day invasions have been strikingly underestimated (Carlton, 2003, 2009). Further, many potential historical introductions remain unquestioned as native species, whereas they should be regarded as cryptogenic species: that is, species that are not yet demonstrably native nor introduced (Carlton, 1996, 2009). Estimating the scale of cryptogenesis is crucial to our understanding of modern marine community ecology and our basic assumptions about and interpretation of

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the natural diversity, biogeography and rate of evolution in the seas (Carlton, 2003).

I estimated the number of cryptogenic species in the North Atlantic Ocean by selecting as model taxa three prominent groups of marine invertebrates: ascidians (Chordata), bivalves (Mollusca) and hydrozoans (Cnidaria). The North Atlantic is relatively well explored; comprehensive biological surveys commenced as early as the mid-19th century and shallow-water benthic invertebrate communities have been extensively studied since. Distributions of individual macroinvertebrate species in these groups in the North Atlantic are therefore relatively well known.

In general, shallow-water invertebrate and algal species in the North Atlantic can have one of four distributional patterns: they can either occur across the entire North Atlantic (amphi-Atlantic), occur only in cold arctic waters, be restricted to one side (Europe) or the other (America), or occur on both sides but not in between and thus have a disjunct distribution. Four models have sought to explain such disjunct patterns: (1) a natural relict distribution following the end of the last glaciations; (2) inadequate taxonomic resolution, suggesting that it is not the same species that occurs on either side of the ocean; (3) natural transoceanic dispersal, without successful colonization in intervening locations; or (4) human-mediated transoceanic dispersal.

Ascidians, epifaunal bivalves and hydrozoans differ in their natural and anthropogenic dispersal potential (Table 1). However, the range of their reproductive and dispersal modes encompasses those of nearly all marine organisms, and therefore, these taxa serve as strong surrogate candidates to represent general biogeographic patterns for the overall marine fauna. All have the potential for natural pelagic dispersal on coastal or oceanic currents, with larval durations of hours to months, all have the ability to raft at some life stage, and all have the potential for human-mediated dispersal. Infaunal bivalves, which are generally not transportable by either natural rafting or in hull fouling, serve both as a control group for epifaunal bivalves and as surrogates for those phyla and classes that do not interface with rafting or hull fouling.

I determined the numbers of native, cryptogenic and known introduced species within and between ascidians, bivalves and hydrozoans in the North Atlantic and then used these data to weigh the evidence for or against the four 'disjunct' models. I further examined the resulting biogeographic, ecological and evolutionary implications of the scale of cryptogenesis for the North Atlantic marine biota overall.

METHODS

Geographic region and habitat boundaries

The geographic region considered here is the North Atlantic Ocean, bordered in the South by Cape Hatteras in the Western Atlantic (35°12′N – 75°31′W), and the Strait of Gibraltar in the Eastern Atlantic (35°58′N – 5°37′W). I focused on shallow-water species occurring in depths of < 100m.

Taxonomic groups

Bivalves, ascidians and hydrozoans were selected because they span a wide variety of habitats and reproductive strategies representative of a broad array of invertebrate phyla, are conspicuous and abundant components of coastal communities, are relatively well studied and differ substantially in their dispersal capabilities (Table 1).

Ascidians are hermaphrodites, and sperm is shed into the sea. Some colonial ascidians can store exogenous sperm for prolonged periods (Bishop & Ryland, 1991). Most solitary species spawn their eggs into the sea, where they are fertilized and develop into tadpole larvae. Some solitary and all colonial forms brood their eggs (Lambert *et al.*, 1995). Eggs develop into larvae that may or may not be able to swim. Larval duration is short, ranging from minutes to several hours, although metamorphosis may be delayed for up to 10 days in

Table 1 Generalized habitat and natural dispersal characteristics of Ascidiacea, Hydrozoa and Bivalvia.

			Bivalvia		
Dispersal mode	Dispersal distance	Ascidiacea	Infaunal	Epifaunal	Hydrozoa
Long-lived larvae (up to months)	Coastal	–	+	+	+
	Transoceanic	–	?*	?*	?*
Short-lived larvae (hours to days)	Coastal	+	–	–	+
Rafting	Coastal	+	rare†	+	+
	Transoceanic	?‡	?‡	?‡	?‡
Hull fouling	Coastal and transoceanic	+	rare†	+	+
Ballast water	Coastal and transoceanic	rare§	+	+	+

*The ability of larvae of shallow-water taxa to successfully complete transoceanic dispersal is largely unknown, but the known length of larval duration generally falls far short of the calculated cross-basin transit times of ocean currents in the North Atlantic Ocean (Scheltema, 1971; Fratatoni, 2001).
†Juveniles of some infaunal bivalves (*Mya arenaria* and *Gemma gemma*) have been found in heavy fouling on moored ships (J. T. Carlton, pers. comm.) and may also have occurred in shipworm burrows.
‡Successful transoceanic dispersal by rafting of these shallow-water taxa is not known.
§Ascidian larvae (of solitary species) of more than 10 days of age have been found in ballast water but are rare (Carlton & Geller, 1993).

some species (Svane & Young, 1989), a trait potentially important for overseas ballast water transport (Carlton & Geller, 1993). With this exception, owing to the short time larvae are free-swimming, the natural dispersal capacity of ascidians is limited, except by rafting.

In contrast, bivalves (that can either be dioecious or hermaphroditic) have a pelagic larval phase that can last days to weeks. Some species brood their offspring (e.g. *Lasaea*) and release them either as pelagic larvae or as benthic juveniles. Delayed metamorphosis occurs in the absence of suitable substrate for settlement and can extend the free-swimming larval phase to months (Thorson, 1950). Byssus drifting is universal in bivalves, except in Ostreacea and Teredinidae. Growth is slowed down, shell thickening is delayed to retain buoyancy, and an intermediate filter-feeding mechanism is present during the byssus drifting stage (Sigurdsson *et al.*, 1976). Bivalves are thus potentially capable of dispersing over large spatial scales.

The hydrozoan life cycle is complex and typically consists of three phases, with varying dispersal potential. The polyp phase is generally spent attached to a biotic, abiotic or artificial substrate and is dependent on the mobility of the substrate for dispersal. Polyps reproduce asexually by the budding of medusae, which are either released or retained as fixed medusoids or sporosacs. Free-swimming medusae have a life span of a few days up to many months, during which they reproduce sexually and form larvae. The ciliated planula larvae spend hours to days in the water column. Hydroids are thus potentially capable of broad dispersal. However, some species of Hydrozoa brood their larvae, restricting the free-swimming larval phase (Ruppert & Barnes, 1994).

Comparing epifaunal and infaunal bivalves

Most ascidians, hydrozoans and bivalves have a sedentary adult phase, often attached to a substrate. Long-distance dispersal by the juvenile or adult phase is possible by rafting on natural floating substrates, such as algae or pumice, or with anthropogenic vectors such as shipping (fouling, rock ballast, ballast water) or shellfish translocations. To determine the relative importance of long-distance dispersal by larvae versus dispersal of the adult phase on rafts, ships or shellfish in crossing the open ocean barrier, I use infaunal bivalves as a control group. Infaunal (burrowing) bivalves are generally unlikely candidates for dispersal by rafting or on ships' hulls (but see Table 1 for exceptions, such as *Mya arenaria*, in infaunal bivalve that was possibly introduced as juveniles in hull fouling, or as larvae in the bilge water of Viking vessels). The larvae of infaunal bivalves may be transported in ballast water and introduced outside their native range. Around 1880, the use of ballast water became common practice, and it is now regarded as one of the major anthropogenic vectors of introduction (Carlton, 1985). Because it has been in effect for a relatively short period in time, for well-known groups such as bivalves, we generally know which species have been introduced by ballast water. Trans-oceanic oyster transports also commenced in the late 19th century (Carlton & Mann, 1996), and for these, we also generally know which infaunal bivalve species accompanied these translocations. The distributions of infaunal bivalves before 1880 are therefore presumed to be natural distributions that are not influenced by historical shipping.

The effect of the Pleistocene glaciations on distribution patterns is assumed to be similar for infaunal and epifaunal bivalves, and comparing their relative numbers of disjunct distributions will reveal whether long-distance dispersal of larvae is a strong mechanism for the creation of disjunct distributions.

Taxonomic, dispersal potential and biogeographic status data

I considered all species of Hydrozoa, Ascidiacea and Bivalvia in North Atlantic shallow waters by reviewing literature and consulting taxonomic experts. For each species, I included information on its world-wide distribution (if applicable), and where possible, the depth range, reproduction, life history characteristics and dispersal capabilities. Species were then assigned to a generalized distribution category in the North Atlantic: Europe, America, Arctic [only occurring in the Arctic realm (Spalding *et al.*, 2007)], amphi-Atlantic or disjunct. Disjunct species occur on both sides of the North Atlantic but are absent from one or more coastal regions of the Arctic realm, i.e. Spitsbergen, Iceland, Greenland and northern Canada, resulting in an interrupted distribution pattern.

Rafting potential (Thiel & Gutow, 2005) was based on either actual observations or on inferences based on distribution (the distinction between the two being noted). The potential for transport by hull fouling was based on actual observations, not on reports of presence on other artificial substrates such as pontoons, pilings or piers (although this was also noted). The potential for natural transoceanic larval dispersal was based upon the known life histories. From the combined species characteristics and distribution pattern and based upon palaeontological, archaeological, historical, biogeographic, habitat, phylogenetic and genetic data, a species status was assigned as follows[1]:

1. *Introduced*: not historically present (in Europe or America) and clearly linked to an anthropogenic vector.

2. *Cryptogenic*: disjunct distribution, history of introduction in other regions, association with an anthropogenic vector, and other life-history characteristics that would facilitate introduction by humans, but lacking at this time a clear historical record of distribution.

3. *Native*: demonstrably historically present at the locations where it now exists, and biology and ecology leave no reason to doubt the naturalness of the distribution.

4. *Other*: an unclear or debated taxonomy, wrongly identified in many places, distribution based on very few records, or ranging to warmer or deep waters. Species that occur both on

[1]The species status assigned here does not necessarily agree with the conclusions in the cited references.

coasts and in deeper waters may in fact have continuous distributions in the North Atlantic and are therefore not regarded as truly disjunct species. This also applies to species that extend their range into the (sub)tropics: larval durations in warmer waters are typically longer (Thorson, 1961), the expanse of ocean that separates the continents is narrower, the surface oceanic current system may allow dispersal in both directions, and species may have survived in refugia in the tropics. The 'other' category thus contains species that are not strictly disjunct; there are other reasons than characteristics of their dispersal potential for a reportedly disjunct amphi-Atlantic distribution pattern.

Individual species can be introduced on one side of the Atlantic and have an unclear origin and thus be cryptogenic on the other coast. To these species, an introduced status was assigned, because anthropogenic dispersal across the Atlantic is responsible for the creation of the disjunct distribution pattern.

RESULTS

We reviewed a total number of 185 ascidians, 448 bivalves (299 infaunal and 149 epifaunal bivalves) and 397 hydrozoans. Of the total reviewed biota of 1,030 species, about 10 per cent (105 species) of all ascidian (see Table S1 in Supporting Information), bivalve (see Table S2) and hydrozoan (see Table S3) species have a disjunct distribution in the North Atlantic.

The species from the other distribution categories (America, Europe, Arctic and amphi-Atlantic) are included in Tables S4 (ascidians), S5 (bivalves) and S6 (hydrozoans). Proportions of disjunct distributions (Fig. 1) are 4.5% in bivalves, 8.7% in ascidians and 17.1% in hydrozoans. Within bivalves, the proportions differ between groups; 3.0% of the infaunal bivalves and 7.4% of the epifaunal bivalves have a disjunct amphi-Atlantic distribution.

Of the 105 disjunct species, 21 are known introductions, 34 are cryptogenic, and only 5 are here considered to be naturally distributed but disjunct on the two sides of the North Atlantic. Forty-five species are considered here to be not strictly disjunct and are assigned to the 'other' category. In terms of percentage composition by group, 39.7% of hydrozoans are cryptogenic, far more than bivalves and ascidians, and 44.1% of hydrozoans are in the 'other' category (Fig. 2).

Disjunct species

Of the 17 species of disjunct ascidians, 11 have been observed in fouling communities; three of these have also been observed on rafts. Eight species are known introductions, three of which were introduced from Europe to America by ships (*Diplosoma listerianum*, *Botryllus schlosseri* and *Ascidiella aspersa*). Most of the introduced ascidians originate in the North Pacific. Four species are cryptogenic: *Didemnum candidum*, *Molgula manhattensis*, *Ciona intestinalis* sp. B and *Perophora viridis*. *Cnemidocarpa mollis* is the only species with a 'natural' disjunct amphi-Atlantic distribution; there are no indications that it has been introduced, nor is it known to be associated with any anthropogenic vectors (Fig. 2, Table S1).

Twenty bivalves have a disjunct distribution (Fig. 2, Table S2). Of these, 11 are epifaunal and nine are infaunal. Six species are recorded from fouling assemblages: five epifaunal bivalves and the infaunal *Mya arenaria*, of which juveniles are sometimes found in fouling communities.

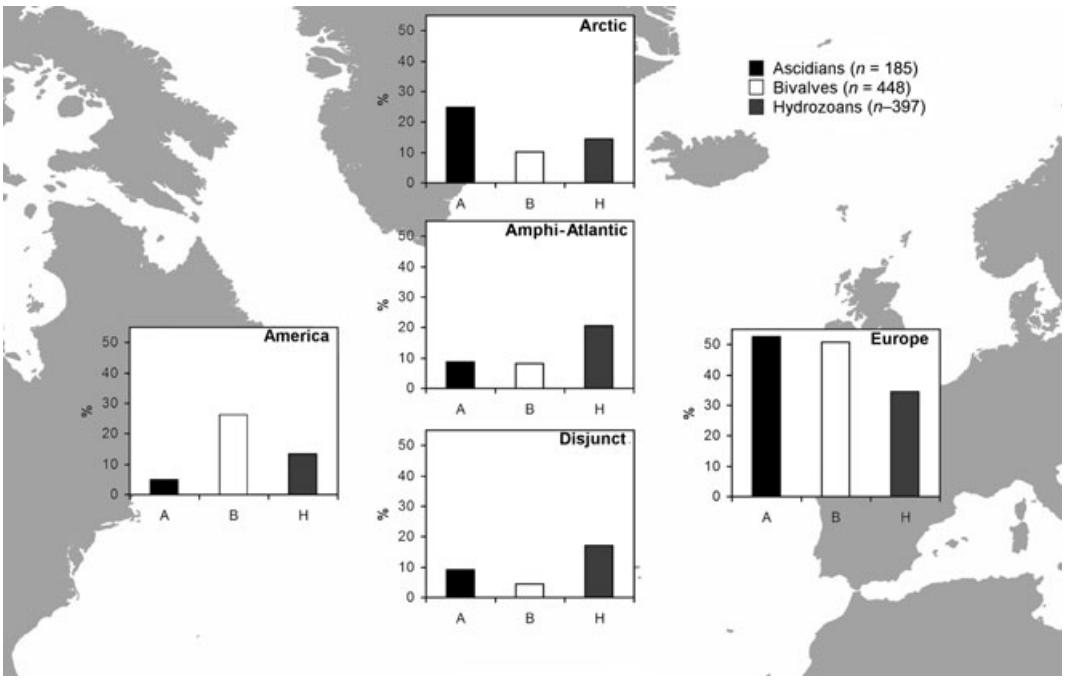

Figure 1 Relative numbers of species per group (ascidians, bivalves and hydrozoans) for each distribution category.

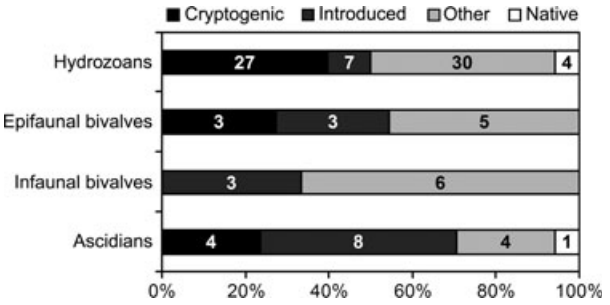

Figure 2 Proportions of cryptogenic, introduced, other and native species with a disjunct distribution for each group: ascidians (n = 17), infaunal bivalves (n = 9), epifaunal bivalves (n = 11) and hydrozoans (n = 68). Absolute numbers per category are indicated in the bars.

Three disjunct epifaunal bivalves are introduced (*Geukensia demissa*, *Mytilopsis leucophaeata* and *Ostrea edulis*). Three are cryptogenic: *Neopycnodonte cochlear*, a common fouling species; *Lasaea adansoni*, a hermaphroditic brooder with direct development, with a complex history of possible cryptic speciation, rafting and human-mediated introductions (Ó Foighil & Jozefowicz, 1999); and *Mytilus trossulus*, which has a natural population in the Baltic Sea but has also been introduced from America to Europe (Väinölä & Strelkov, 2011). Three infaunal bivalves were deliberately or accidentally introduced (*Mya arenaria*, *Ensis directus* and *Mercenaria mercenaria*). Importantly, there are no cryptogenic infaunal bivalves, nor are there any naturally disjunct bivalves.

Of the 68 species of disjunct hydrozoans, seven are inferred introductions by means of ship hull fouling (*Bougainvillia rugosa*, *Nemopsis bachei*, *Eudendrium carneum*, *Cordylophora caspia*, *Blackfordia virginica*, *Gonionemus vertens* and *Maeotias marginata*).

Nineteen species have been observed on ship hulls; four of these have also been recorded as rafting, and for four more, rafting had been assumed based on their disjunct distributions (Table S3). Six species have been reported rafting but have not been recorded from ship hulls; two of these are obligate rafters on pelagic gastropods (*Kinetocodium danae* and *Pandea conica*), leaving four species with a possibly natural disjunct distribution. Twenty-seven hydrozoans are cryptogenic (Fig. 2); examples include *Obelia dichotoma*, *Garveia franciscana* and *Sarsia occulta*. I did not find large differences in the combined proportions of disjunct and amphi-Atlantic distributions for medusa-releasing (40.9% of 132 species) or medusa-retaining (39.5% of 215 species) Hydrozoa. Widely distributed species did not more frequently have a free-swimming medusa than species with a narrow geographic distribution.

DISCUSSION

The proportion of species with a disjunct distribution (10%) is similar to numbers found by other authors who have studied the relationship between the European and American boreal fauna. Based upon what little was known at the time of general marine invertebrate distributions, Lovén found 8% shared species between Europe and America (Lovén, 1846 in Briggs, 1995). Briggs (1974) estimated that 24% of North Atlantic fish were disjunct. Huus (1927) described four disjunct amphi-Atlantic ascidians, and only for *Cnemidocarpa mollis* did he conclude that shipping was not responsible for the disjunct distribution, in accordance with the present results. Naranjo *et al.* (1998) conclude that the number of amphi-Atlantic ascidians is low and corresponds with typically cosmopolitan species associated with anthropogenic vectors. Estimates for the number of amphi-Atlantic molluscs vary, due in part to analyses being based on differing taxonomic groups. Coomans (1962) found that 18% of 'native' American molluscs also occur in Europe. Of the American Nudibranchia and Cephalaspidea, 25–30% have a disjunct distribution (Franz, 1970). Vermeij (2005) analysed current geographic distributions and the fossil (Pliocene) record of shallow-water shell-bearing molluscs in cool-temperate North Atlantic waters. He included the disjunct species in the amphi-Atlantic category and found that 23% of species had a disjunct or continuous amphi-Atlantic distribution, compared to 13% of the bivalves (4.5% disjunct and 8.3% amphi-Atlantic) in this study, but Vermeij included fossil species that may now have become extinct (in part of their range).

Disjunct amphi-Atlantic distributions are thus not very common, and, as noted above, fully 43% (45) of the 105 disjunct species are not strictly disjunct. The four models that have been proposed to explain disjunct distribution patterns are discussed below.

Glacial relict distribution

During the Last Glacial Maximum (LGM), *c.* 21,000 BP, temperate species ranges were contracted in glacial refugia owing to ice cover and a drop in sea level. After the LGM, both Atlantic coasts were recolonized from these refugia, of which most were located in the south (Maggs *et al.*, 2008). On the North American coast, species that are obligatory hard substrate species would have had either to retreat to a northern refuge, meaning that they were capable of surviving low temperatures and would now be likely to occur in the Arctic as well, or to survive in a southern refugium, where hard substrates are rare. Therefore, recolonization from refugia is assumed to also have taken place across the Atlantic Ocean, from Europe to America (Briggs, 1974; Vermeij, 2005), which is in conflict with the direction of surface currents (Fratatoni, 2001). In cold temperate to Arctic waters, there is a possibility of east-to-west dispersal (Dawson *et al.*, 2005), using Iceland and Greenland as stepping stones, resulting in amphi-Atlantic distributions (Wares & Cunningham, 2001; Wares, 2001), but not in the disjunct distributions of the strictly temperate species considered here.

The only explanation that remains for these disjunct species is the existence of relict populations on both coasts owing to extinction in northern regions during the LGM, with some

resulting expected level of genetic divergence over time and a signature of a long evolutionary history on both coasts. There are no convincing examples of this scenario. Many studies simply assume that intermediate extinctions, although any direct evidence for such is absent, are responsible for the disjunct distributions we see now. The influence of anthropogenic transport is often viewed as having minor influence, which biases conclusions.

Distinguishing between anthropogenic introduction and glacial relict populations proves to be difficult (Haydar *et al.*, 2011). Newly colonized ranges, be they after the LGM or after an introduction event, were long thought to be characterized by low haplotype diversities caused by population bottlenecks owing to small founding populations (Hewitt, 1996; Holland, 2000). However, they can harbour relatively high genetic diversity owing to admixture after post-glacial invasion from more than one refugium in the case of natural expansion (Maggs *et al.*, 2008) or multiple introductions in the case of anthropogenic dispersal (Roman & Darling, 2007), in both cases potentially leading to increasing diversity levels over time. Also, depending on the parameters and analytical models chosen, genetic data can be interpreted to lead to opposing conclusions (Chapman *et al.*, 2007; Cunningham, 2008).

In the present study, it is striking that there are no cryptogenic or naturally disjunct infaunal bivalves, although the effect of the LGM would have been the same for all taxonomic groups. The 'naturally' disjunct species are not *demonstrated* to be glacial relicts, nor are they confirmed to be the same species occurring on both coasts, but there was no evidence to assign them to introduced, cryptogenic or other categories. However, it remains possible that genetic analysis will reveal that what is thought to be one species will be two or more.

Taxonomic artefact

Molecular genetic studies have resulted in the discovery of cryptic species complexes across all taxonomic groups and in all habitats. The marine realm harbours an especially high number of cryptic species because of the high species richness and complex inter-specific interactions (Bickford *et al.*, 2007). Many cosmopolitan species appear not to be so when analysed with molecular methods. An example is the ascidian *Ciona intestinalis*, a model organism for developmental and evolutionary studies, which is actually a species complex, consisting of at least four species that do not differ distinctly in morphology, although they do have distinct geographic distributions (Zhan *et al.*, 2010). *Ciona 'intestinalis'* sp. A and sp. B are invasive: sp. B has a disjunct amphi-Atlantic distribution and is cryptogenic, sp. A is near cosmopolitan but, in the North Atlantic, only occurs at the western end of the English Channel, in both SW England and Brittany, where it co-occurs with sp. B.

Even in a well-studied group such as bivalves, boundaries are not clear and cryptic speciation is not uncommon (Mikkelsen, 2011). The *Mytilus* complex consists of three species: *Mytilus edulis*, *Mytilus galloprovincialis* and *Mytilus trossulus.* In Europe, the three species hybridize in zones of contact and the extent of the differentiation of the species is debated, depending on the genetic marker used (Riginos & Henzler, 2008). *Mytilus trossulus* has a circumpolar distribution, extending into boreal and temperate waters in the North Pacific and also occurring in the Baltic Sea in Europe. The Baltic population is genetically different from the North Pacific populations but is regarded as the same species with introgression of *M. edulis* mtDNA (Rawson & Hilbish, 1998). Furthermore, northern European *Mytilus* populations appear to be composed in part of *M. trossulus* as a result of repeated cryptic invasions, some of which my be the result of human activities (Väinölä & Strelkov, 2011). *Mytilus galloprovincialis* is native in Europe and has been introduced world-wide (Carlton, 1999a). Its introduction in California went unnoticed as it was mistaken for the native *M. trossulus*, whose decline in abundance was masked by the invasion of *M. galloprovincialis* (Geller *et al.*, 1994; Geller, 2002). The additional anthropogenic intentional transport of these mytilids for shellfish culture further blurs species boundaries (Mikkelsen, 2011).

These are but two examples from well-studied species. Especially in less-conspicuous and less-studied taxa, such as the hydrozoans, species complexes doubtless remain to be discovered with the use of molecular tools, and it is thus not unlikely that many disjunct and cryptogenic species are in fact two or more species.

Natural trans-oceanic dispersal

Adaptations such as long-distance dispersal of larvae (Thorson, 1950; Scheltema, 1971), and rafting of juveniles, adults or egg masses on floating substrata (Johannesson, 1988; Thiel & Gutow, 2005) are natural mechanisms that can result in the colonization of distant shores.

Planktonic duration of larvae and dispersal distance were long assumed to be positively correlated, the reasoning being that larvae are passively transported in ocean currents and therefore the longer they are in the plankton, the further they disperse (Scheltema, 1971; Jablonski, 1986). However, retention of larvae in coastal waters is not uncommon (Levin, 2006), and pelagic larval duration is not a good predictor of the magnitude of gene flow and geographic scale of population structure in marine systems (Weersing & Toonen, 2009). On large scales, such as ocean basins, there is no positive relationship between dispersal ability and range size (Lester *et al.*, 2007).

In the present study, these patterns are reflected by a disjunct distribution being less common in bivalves than in ascidians, even though the larval phase of most ascidians typically lasts only minutes to hours, whereas bivalve larvae may spend weeks to months in the plankton. The infaunal bivalves form a control group: they cannot usually be dispersed in hull fouling, nor can they typically be rafted, and long-distance dispersal would only be possible by natural larval dispersal or dispersal of larvae in ballast water. As ballast water

has been in use since *c.* 1880, we generally know which species were introduced by this vector. There are no cryptogenic infaunal bivalves, nor are there any disjunct bivalves for which there is proof that their distribution is a result of natural dispersal (Fig. 2). In hydrozoans, disjunct distributions do not occur more often in species with a free-swimming medusa, and cosmopolitanism is more common in species that do not release medusae (Jackson, 1986; Cornelius, 1992). The data confirm that the presence of an extended pelagic stage in the life cycle does not guarantee widespread natural occurrence of a species.

Natural dispersal by rafting is seen as a successful long-distance dispersal mechanism, in particular for species that have internal fertilization, incubate their offspring or deposit eggs on rafts (Thiel & Gutow, 2005). Dispersal by rafting is potentially more successful than dispersal by planktonic larvae; chances of colonization by the offspring of a brooding female are greater than those of a single larva. Asexual reproduction (e.g. by budding or fragmentation) further increases the survival and establishment success of rafters (Jackson, 1986). Hydrozoans and ascidians are therefore excellent candidates for dispersal by rafting, and hydrozoans are among the most commonly observed taxonomic groups on rafts (Thiel & Gutow, 2005).

The colonial ascidians, which are capable of budding and often brood their larvae, would be expected to more often have a disjunct distribution than solitary ascidians. However, the majority of disjunct species are solitary ascidians that have not been reported to raft. Of the four compound species with a disjunct distribution, three are introduced by humans. The fourth species has not been observed on rafts, but rafting had been inferred based on its disjunct distribution (Thiel & Gutow, 2005).

In hydrozoans, rafting of the hydroid (polyp) stage is often assumed to be the most important dispersive mechanism (Jackson, 1986; Cornelius, 1992). Of the 68 disjunct hydrozoans, 21 have been reported to raft. Of these, seven have also been observed on ship hulls, and for five of these, rafting was inferred from their disjunct distributions. Disjunct distributions are in many cases used as 'evidence' for rafting (Thiel & Gutow, 2005); the possibility of anthropogenic dispersal is often not considered, as noted earlier.

More importantly, all observations of rafting organisms are from coastal rafts. Rafting is no doubt an important means of maintaining population connectivity on smaller spatial scales, e.g. along coastlines, but long-distance rafting has so far not been demonstrated. There is only one study that describes direct evidence for rafting of coastal organisms across several hundred kilometres of the southern ocean (Fraser *et al.*, 2011), but this scale is still not comparable to the thousands of kilometres of Atlantic open water that would have to be crossed. Without direct evidence, genetic, biogeographic, ocean circulation modelling and historical or palaeontological data have to be combined to prove that a disjunct distribution can only be the result of rafting. These studies are rare and fail to convincingly demonstrate the role of rafting in dispersal across ocean basins. Furthermore, those species that raft are also likely to be able to attach to ships.

Human-mediated introduction

Ships are more successful dispersal agents than rafts: they travel relatively fast, provide extensive surface area, are likely to arrive at an amenable habitat and, unlike larvae and rafts, are independent of ocean surface currents. The major vectors for introduction of non-indigenous coastal organisms associated with historical shipping were the solid ballast (mostly rocks and sand from the intertidal) they carried for stability, the shipments of live shellfish that were transported (in particular live oysters that were relaid in recipient waters), and the fouling and boring communities on and in the hull.

Around 1880, rock ballast was replaced by ballast water, which has become a very potent vector in modern times. Because ballast water use and oyster shipments have occurred since the late 19th century, we generally know which larger and taxonomically better-known species were introduced by these vectors. However, great numbers of ships have been sailing across the North Atlantic Ocean since at least 1000 BP, when the Vikings first reached the American Atlantic coast, but only since comprehensive biological surveys began in the mid-1800s have we been able to document the appearance of novel species on either side of the North Atlantic (Carlton, 1989, 2003). Historically, ships were made of wood, travelled at slower speeds and had long port residence times, allowing rich hull fouling communities to develop and increasing the chance of successful introduction and establishment of a permanent population (Allen, 1953). A wooden sailing vessel around 1750 could theoretically carry over 150 species of invertebrates, algae and plants on and in its hull, on the anchor, and in its sand and rock ballast (Carlton, 1999b). Leaky wooden vessels may have additionally carried various life stages of invertebrate species and algae in the bilge water (Carlton, 2011).

Of the disjunct amphi-Atlantic species analysed here, 58.8% of the ascidians, 30.0% of the bivalves and 27.9% of the hydrozoans have been observed on ship hulls. An even larger number occur in fouling communities on man-made structures and on natural and artificial rafts and may therefore also be able to attach to ships. Of all disjunct species, 20.0% have been introduced in part of their range, and the majority of the epifaunal disjunct species have been introduced by ships.

Long-distance dispersal by ships is thus not rare or uncommon: it has profoundly influenced distributions of many species of invertebrates and algae (Carlton, 2003). The archaeological record provides a possibility to detect some earlier invasions, such as the Norse movement of the clam *Mya arenaria* from America to Europe (Petersen *et al.*, 1992). In addition, historical and cryptic introductions in the marine environment are being revealed on a regular basis with the help of molecular tools, e.g. the Portuguese oyster *Crassostrea angulata* was introduced to Portugal from Taiwan (Boudry *et al.*, 1998; Ó Foighil *et al.*, 1998), and the ascidian *Botryllus schlosseri* was probably transported from Europe to America

long ago, but it remains unclear whether it is native to Europe (Carlton, 2005; Lopez-Legentil *et al.*, 2006). In other taxonomic groups, repeated cryptic invasions have also been demonstrated, e.g. in the cosmopolitan bryozoan *Bugula neritina* (Mackie *et al.*, 2006). Bryozoans are a group for which fouling ability is strongly correlated with range, more so than larval development, environmental tolerance, species abundance and the ability to raft (Watts *et al.*, 1997).

CONCLUSIONS

There are at least 34 species of cryptogenic ascidians, bivalves and hydrozoans across the North Atlantic. This is a conservative estimate, as the present analyses omitted all species that now have a continuous distribution across the North Atlantic but may in fact have been carried by ships for centuries to the Faeroes, Iceland, Greenland and Labrador, creating seemingly unbroken distributions that are interpreted to be natural.

Extrapolating this to all invertebrates and algae in the North Atlantic, a reasonable conclusion is that the number of overlooked invasions may be in the hundreds of species. Species that are assumed to be native but have a disjunct amphi-Atlantic distribution are very likely to have been introduced in historical times, as the only scenario that convincingly explains disjunct distributions is the anthropogenic introduction model. Modern-day invasions consist of many taxa that have become abundant ecosystem engineers in marine communities globally (Wallentinus & Nyberg, 2007). There is clearly no reason to assume that cryptogenic species, especially those introduced prior to 1900, are inconspicuous, rare or minor species and that major introductions are only those which we have observed to occur since the 1900s.

The shifting baseline syndrome (Pauly, 1995) applies not just to perceptions of the size and extent of fisheries stocks but to all aspects of the environment. In marine ecosystems, a 'natural state' has often been assumed, based upon the 'foundation' studies of the first marine biologists to arrive in a region (Carlton, 2009). We can no longer ignore the fact that the structure of many North Atlantic marine communities has been highly influenced by overlooked historical invasions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Disjunct amphi-Atlantic Ascidiacea.

Table S2 Disjunct amphi-Atlantic Bivalvia.

Table S3 Disjunct amphi-Atlantic Hydrozoa.

Table S4 European, American, Arctic and amphi-Atlantic Ascidiacea.

Table S5 European, American, Arctic and amphi-Atlantic Bivalvia.

Table S6 European, American, Arctic and amphi-Atlantic Hydrozoa.

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BIOSKETCH

Deniz Haydar is interested in how the biogeography of benthic marine organisms is changed by human activities, in particular by shipping and shellfish translocations. She aims to elucidate consequences of historical, overlooked introductions on patterns of distribution and genetic diversity, by integrating ecological and phylogeographic methods and historical resources such as museum collections and archives.

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